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Environmental distribution of Bathonian (Middle Jurassic) neoselachians in southern England

Charlie J. UNDERWOOD & David J. WARD

Abstract

Within the Bathonian (Middle Jurassic) a wide range of depositional environments were present across Britain. Within this dominantly carbonate shelf setting, there is a general palaeoenvironmental transition from open marine shelf in the south of England, to marine and non-marine lagoons in south-central England. Isolated teeth of neoselachians are frequent at several localities within a range of marine and lagoonal facies. Extensive bulk sampling has allowed teeth from over 20 neoselachian taxa to be recovered from several distinct facies. The distributions of many species suggest that they were strongly environmentally controlled, with few taxa being commonly present within both open marine and lagoonal settings. Some taxonomic groups appear to have been restricted to specific environments, with hexanchids and palaeospinacids only being recorded within open marine facies. Within other groups, environmental segregation is at generic and specific level, with different species of *Protospinax*, orectolobids, batoids and scyliorhinids being recorded within different facies. The differential distribution of neoselachians within the Bathonian demonstrates that the initial phase of neoselachian radiation during the late Early and Middle Jurassic was accompanied by diversification into a wide range of ecological niches. This greatly increases our understanding of the mechanisms and timing of neoselachian radiation and Jurassic fish palaeoecology.

Introduction

The early phases of radiation of the neoselachians during the Late Triassic to Middle Jurassic constitutes one of the most dramatic radiation events within the fishes, seeing the appearance of many extant taxonomic groups. Despite the importance of this interval, no study has investigated the environmental distribution of these groups and role played by environmental segregation on neoselachian evolution. The range of palaeoenvironments present within the British Bathonian, and the general abundance of neoselachian remains within it, would suggest that the Bathonian would comprise an ideal study area for a study into early neoselachian palaeoecology.

Within northern Europe, the Bathonian was a time of low sea levels and high carbonate production. Across southern Britain, large areas of shallow water conditions became cut off from open marine environments by the development of extensive oolite shoals, producing extensive lagoon complexes. The majority of the Bathonian in southern Britain is included into the Great Oolite Group, within which, despite this name, oolites are only a relatively minor component of the succession. The Great Oolite Group is dominated by neritic mudstones near the English South Coast, with lagoonal micrites and marls dominating further to the north east in the northern Cotswold Hills and Oxfordshire.

Sampling

The diversity of palaeoenvironments present within the British Bathonian give rise to a suite of facies which may be differentiated on lithological and faunal grounds. Fluctuating environmental conditions, in combination with a general southerly progradation of facies, typically result in a number of facies being accessible at any particular field locality. In all, faunas from nine readily recognisable facies were studied, with sampling roughly formed a transect from dominantly open marine facies in the south-west to lagoonal facies in the north-east (see Fig. 1).

Neritic mudstone facies: The bulk of neritic mudstones within the study area consist of expanded silty mudstones with very little fauna. For this reason, the fauna from this facies was obtained from a single fossiliferous horizon comprising an oyster-belemnite shell bed within a dark fissile mudstone. This is exposed as a fault-bounded block at Watton Cliff, Dorset.

Brachiopod limestone facies: Hiatal and inner shelf facies typically comprise nodular micrites with interbeds of calcareous mudstone. These contain rich and diverse assemblages of brachiopods and other invertebrates, often in life position. Three samples were collected at two localities, a temporary exposure at East Cranmore, Avon (see SAVAGE 1977 for regional details) and Watton Cliff, Dorset (see ARKELL 1947).

Tilestone facies: This facies, typified by the well known Stonesfield Slate, comprises laminated and low angle cross bedded silty and micro-oolitic limestones. Shelly fossils are restricted in diversity and trace fossils are represented by uncommon *Skolithos*. This facies represents a suite of nearshore to lower shoreface environments. Samples were collected at Hampen Cutting, Gloucestershire (SUMBLER & BARRON 1996) and non-systematically collected material has also been studied from several other sites.

Oolite shoal facies: Cross bedded oolitic packstones and grainstones deposited within oolite shoals and bars are common within the British Bathonian. They typically contain few fossils, but some abraded neoselachian teeth were observed from oolite samples from Huntsman's and Brockhill Quarries, Gloucestershire, and samples of a shelly channel lag at nearby Hampen Cutting.

Shell bank facies: Bivalve shell banks with a muddy matrix containing abundant ooids were sampled at Hampen Cutting and Woodeaton Quarry, Oxfordshire (HORTON et al. 1995). Three oyster dominated and one mixed bivalve shell bed samples were collected. These probably represent outermost lagoon deposits with fully marine conditions and ooids washed in from the nearby barrier shoal.

Saline lagoon facies: Shelly marls alternating with pale micrites were sampled at a number of horizons at Woodeaton Quarry. These low-energy deposits contain diverse invertebrate faunas and represent fully marine lagoon environments.

Restricted lagoon facies: Green and grey mudstones, often associated with rootlet horizons, were sampled at several levels at Woodeaton and Kirtlington (McKERROW et al. 1969) Quarries, Oxfordshire. The invertebrate fauna is of low diversity and contains forms tolerant of low salinity, such as oysters, corbulids and *Placunopsis*.

Transported lagoonal facies: Within the late Upper Bathonian, cross bedded bioclastic limestones dominate over much of the outcrop within the study area. Variably oolitic packstones containing transported and faunally mixed invertebrate assemblages were sampled at various levels at Woodeaton Quarry. At this site, these limestones contain wave ripples and interbed with green, occasionally rooted, mudstones, therefore suggesting lagoonal or very shallow water deposition.

Transported open marine facies: Several samples were taken from unlithified patches within a unit of cross bedded bioclastic limestone within the open marine silts of Watton Cliff. This contains a diverse and mixed invertebrate fauna, including open marine elements

such as the crinoid *Apiocrinites*. This unit is well known for its marine, freshwater and terrestrial vertebrate fauna (e.g. WARD in DINELEY & METCALF 1999).

The majority of the material studied was obtained by sieving bulk samples of mudstones and marls, with some additional material extracted from limestones by acid digestion. Bulk samples for sieving were typically 20 to 100 kg dry weight. These were oven dried and sieved through a 320µm mesh in an automated sieve as described by WARD (1981). Carbonate material was removed from the residue by dissolution in 15% acetic acid. Limestones were dissolved in 10% formic or 20% acetic acid (the former being faster in dissolution of compact lithologies). The insoluble residue was removed regularly to prevent possible acid damage to specimens.

Acid-insoluble residues were picked under a binocular microscope. There were few neoselachian teeth in the 1mm sieve fraction. The 500 µm fraction yielded the greatest number of neoselachian teeth, but numerous small teeth were also present in the 355µm fraction.

The yields of neoselachian teeth were highly variable between samples, even those of similar lithology. Mudstones yielded between 0.1 and 11 teeth per kilo (2 to 4 teeth per kilo being typical). Limestone samples yielded between 4 and 10 teeth per kilo. In total nearly 7000 neoselachian teeth were studied.

In addition to material collected during this study, material in museum collections was also studied. This particularly included material in The Natural History Museum, London and material jointly collected by one of us (CJU) with Sara METCALF.

Neoselachian distribution

Taxonomic study of Bathonian sharks and rays is still ongoing, and as such much of the nomenclature used here has been left open. The results of this work will be published elsewhere. This lack of taxonomic work has not, however, prevented analysis of the palaeoecology of these assemblages. A summary of the distribution of neoselachians is given in Fig. 2.

Palaeospinaciformes: Two species of *Synechodus* were recorded during this study. These appear to have strongly favoured open marine environments, with no teeth being recorded within lagoonal facies. *Synechodus* sp. was found within both neritic mudstone and brachiopod limestone facies, forming up to 15% of the neoselachian fauna. A single specimen probably referable to *Synechodus levis* (WOODWARD) was also recorded. Although no palaeospinacid teeth were recovered from shallow marine tilestone facies during this study, several large teeth of *Synechodus levis* are present in museum collections. It is likely that the large size of teeth of this species and the extensive collecting from the 'Stonesfield Slate' during the nineteenth century have led to the overrepresentation of this species within an environment where it was probably very rare. Several specimens of aff. *Welcommia* sp. were recorded as rare elements from both neritic facies.

Hexanchiformes: Rare examples of a single species of hexanchid were recorded during this study. These were recorded exclusively from neritic facies, with no specimens being recorded from other samples.

Heterodontiformes: The three species of heterodontid encountered during this study had rather different distributions, with one species being present in most facies. *Paracestracion* sp. 1. appears to have had a very cosmopolitan distribution. It is present as a frequent member of the lagoonal assemblages (12 to 14%), as well as more rarely within neritic shale facies (associated with a single specimen of *Paracestracion* sp. 2.). *P.* sp. 2 is rare or absent within the Upper Bathonian transported assemblages. *Heterodontus* sp. is present as a rare element within normal marine lagoonal facies, but is common within Upper Bathonian transported assemblages.

Orectolobiformes: Of the five orectolobid taxa recovered, orectolobid sp. 1 was the only taxon recorded from within lagoonal environments. Present within all lagoonal facies, as well as within the Upper Bathonian transported assemblages, teeth of this species never comprise the commonest element in the assemblage, typically forming up to 12% of neoselachian teeth. It was not recorded from open marine or nearshore facies. Conversely, orectolobid sp. 2, *Palaeobrachaelurus* sp. and ? *Orectoloboides* sp. and the single specimen of orectolobid sp. 3 were only encountered within neritic facies. Whilst orectolobid sp. 2 formed similar proportions within both neritic mudstone and brachiopod limestone facies, ? *Orectoloboides* sp. was found to be more common within neritic mudstone facies, where it makes up 20% of the teeth recovered, but far less so within the brachiopod limestone facies where it comprises 3% of the fauna.

Carcharhiniformes: The distributions of the taxa of 'scyliorhinid' recorded during this study show strong palaeoenvironmental control. Teeth of *Palaeoscyllium* sp. were found only in shallow marine deposits, both within the outer lagoon oolitic shell bank facies and the shallow marine tilestone facies. Abraded teeth were also found within palaeogeographically intervening oolite shoal deposits. This taxon is also frequent within the open marine transported facies. 'scyliorhinid' sp. 1 was commonly encountered within all lagoonal facies, on occasion as the dominant selachian element (to over 50% of the assemblage). It is also present, if rare, within open marine facies. Not encountered within any lagoonal sample, 'scyliorhinid' sp. 2 was found as an uncommon element within neritic shale and brachiopod limestone facies, as well as fairly commonly within the transported open marine facies. ? *Palaeocarcharias* sp. is known only from two abraded teeth from the marine transported facies.

Protospinaciformes: Large numbers of teeth were collected from all three of the recorded species of *Protospinax*. Despite the almost ubiquitous occurrence of the genus, frequently as the dominant neoselachian taxon, the three species occur to an almost complete exclusion of each other within any sample. *Protospinax* sp. 1 was found to be the dominant taxon within the neritic shale and brachiopod limestone facies, being absent elsewhere. *Protospinax* sp. 2. was recorded from outer lagoon oolitic shell bank (where it can constitute over 75% of the fauna), oolite shoal, tilestone and transported facies to the virtual or complete exclusion of other species. *Protospinax* sp. 3 is present, albeit as a rather uncommon element, within most lagoonal facies.

Rajiformes: Of the three species of batoid recognised, *Belemnobatis* cf. *moorbergensis* (THIES, 1983) was the most widespread, its presence within all facies making it the most cosmopolitan neoselachian studied. It typically forms a frequent but not dominant neoselachian element, although it may be dominant within higher energy tilestone and oolitic facies. *Spathobatis* sp. appears to have had a similar distribution to *Palaeoscyllium* sp., being most abundant within marine lagoonal, tilestone and shelly transported facies. Rhinobatid sp. was recorded as a rare component of the neritic shale and brachiopod limestone facies.

Controls on neoselachian distribution

There are a range of environmental variables that are likely to have influenced the distribution of early neoselachians. Water depth, temperature, salinity and availability of food are as likely to have influenced neoselachian distribution in the Bathonian as today. It is also likely that the nature of the substrate could have strongly influenced the occurrence of benthic taxa, whilst certain taxa are likely to have been better adapted to thrive in fast currents or turbidity.

Many taxa were recorded only from neritic facies, including *Synechodus* sp., hexanchiforms, several orectolobids and *Protospinax* sp. 1. As well as greater water depth, these offshore facies were deposited under conditions of low energy near the seafloor, stable temperature and salinity and availability of diverse food items. Several taxa were only

abundant in lagoonal facies, such as 'scyliorhinid' sp. 1 and *Protospinax* sp. 2, although only one, orectolobid sp. 1, was restricted to them. Uncommon examples of many of these lagoonal taxa within neritic facies suggest that they were probably cosmopolitan in their distribution, such as *Paracestracion* sp. 1 and *Belemnobatis* cf. *moorbergensis*, able to exist in a wide range of conditions but thriving in lagoons due to a lack of competition.

In addition to taxa restricted to either open marine or lagoonal facies, several species (*Palaeoscyllium* sp., *Protospinax* sp. 2, *Heterodontus* sp.) are restricted to facies adjacent to the oolite shoals, as well as within the transported facies. It is possible that these forms were restricted to shallow water but intolerant of the variable salinities of the inner lagoons. It is also possible that these benthic taxa were in some way substrate controlled, being restricted to oolitic, sandy and shell gravel substrates and avoiding muddy conditions.

Little is known of the possible diet of early neoselachians, although tooth functional morphology and degree of wear may give indirect evidence. Within the species of *Protospinax*, it is likely that the three species differed somewhat in their diets despite rather similar dentition. Teeth of *Protospinax* sp. 1 rarely show significant wear, whereas moderate to intense wear is typical in the other species. Wear is especially evident in *Protospinax* sp. 3, where no unworn teeth were recorded, and a major wear facet is invariably present along the occlusal edge of the teeth. It is therefore evident that within the same genus there are species utilising different foods; *Protospinax* sp. 1 feeding on soft bodied prey and *Protospinax* sp. 3 having a diet including shelled animals.

Comparisons with other assemblages

With a few notable exceptions (e.g. THIES 1983, CANDONI 1995, DELSATE & THIES 1995, REES 2000, UNDERWOOD 2002), very little systematic sampling for neoselachian remains has been carried out within Jurassic sediments, and few of these studies have recorded the sedimentological and palaeoenvironmental context of the sample sites. Studies of pre Toarcian sites have only yielded low diversity faunas of palaeospinacids, hexanchids and the probable stem group galeid *Agaleus* (BIDDLE 1993, DELSATE & DUFFIN 1993, REES 1998, 2000, WARD in DINELEY & METCALF 1999). Several faunas containing more diverse elements have been described from the Toarcian, Aalenian and Bajocian by DELSATE & THIES (1995), and THIES (1983, 1989, 1993). In addition to palaeospinacids (*Synechodus* or *Paraorthacodus*), *Welcommia*, *Protospinax*, *Paracestracion*, several taxa of orectolobids and batoids are commonly present. The small amount of published palaeoenvironmental information suggests that all of these faunas were recovered from hiatal offshore mudstones. In contrast, YOUNG (1982) recorded only 3 specimens of *Paracestracion* from a Bajocian lagoonal facies containing coral patch reefs. Neritic shales of the British Callovian (THIES 1983, MARTILL 1991) have yielded assemblages dominated by *Protospinax*, *Paracestracion*, varied orectolobids and *Belemnobatis*, along with rarer hexanchids and *Sphenodus*. Palaeospinacids do not appear to be common within the typical organic rich mudstones, but are frequent in more silty and calcareous facies (CJU, pers. obs.). Studies of faunas from the neritic Kimmeridgian (CANDONI 1995, UNDERWOOD 2002) also contain palaeospinacids, heterodontids, *Protospinax*, and 'rhinobatids', as well as scyliorhinids and *Squatina*. Although present, the diversity of orectolobids is somewhat lower than within Bathonian and Callovian assemblages.

Kimmeridgian faunas from restricted lagoon settings (THIES 1983, 1995) are dominated by batoids with rare examples of other neoselachians. This batoid dominated assemblage is also present within the Kimmeridgian Cerin plattenkalk (SAINT-SEINE 1949) and the lagoonal Tithonian of western France (CANDONI 1995). A further assemblage comprising common batoids and no other neoselachians was recorded from low salinity lagoon deposits in the basal Cretaceous (UNDERWOOD & REES 2002).

The diverse neoselachian faunas of the Solnhofen and Nusplinger plattenkalks are unlike that recorded elsewhere in the Jurassic. They probably represent allochthonous mixed assemblages of lagoonal, reefal and open marine taxa (VIOHL 1996).

It is evident that the general composition of Bathonian assemblages within neritic facies is very similar to that recognised at other localities throughout the post-Pliensbachian Jurassic, as well as within the Early Cretaceous (UNDERWOOD et al. 1999). Toarcian to Bajocian assemblages differ from those in the Bathonian only in lacking carcharhinids. The first record of *Squatina* in Kimmeridgian assemblages marks the only post-Bathonian appearance of a major neoselachian taxonomic group within the Jurassic.

With the exception of three teeth from the Bajocian, no Lower or early Middle Jurassic neoselachians have been recorded from lagoonal sediments, lagoonal faunas therefore remaining almost unknown. It is unclear whether the batoid dominated lagoonal assemblages of the Kimmeridgian and Tithonian differ from higher diversity Bathonian faunas due to representing more restricted environments than studied here, or whether the dominance of batoids records their increasing adaptation to these habitats.

Conclusions

This study clearly demonstrates the presence of very different neoselachian faunas within different palaeoenvironments in the Bathonian, and for the first time allows for the recognition of strong palaeoenvironmental preferences amongst early neoselachians. Few of the neoselachian taxa recognised were commonly present within both lagoonal and open marine environments. Other species were either restricted to lagoonal, nearshore or neritic settings. Obvious faunal mixing suggests that the palaeoenvironmental preferences of taxa within the transported facies are less clear, although the differential distribution of 'scyliorhinids' does suggest a relationship between faunas and depositional site. Taxa recorded within lagoonal facies differ from those within neritic facies at specific and possibly generic level, with all lagoonal taxa having congeneric or familial relatives within offshore assemblages. This is not reciprocated, with species from groups such as the Hexanchiformes and Palaeospinaciformes being absent within lagoonal settings.

Neoselachian orders only known from offshore settings (Hexanchiformes and Palaeospinaciformes) are well known from similar environments throughout the Early Jurassic. Conversely, groups also known within lagoonal environments are only known in neritic sediments from the Toarcian onwards, with several groups of neoselachians apparently appearing synchronously in the Early Toarcian. For this reason, it may be that this perceived sudden appearance of neoselachian groups is due to their migration from lagoonal to shelfal environments. It is therefore possible that after the initial radiation of the galea and squala producing taxa inhabiting open marine conditions (such as *Agaleus* and hexanchiforms respectively), subsequent radiation of the "crown group" clades of both groups occurred within lagoonal environments during the Early Jurassic.

The restriction of many taxa to particular environments may greatly effect the perception of the diversity of Jurassic neoselachians, as no single sample locality will produce more than a restricted sample of the species present. A clear representation of neoselachian diversity can therefore only be gained if a range of palaeoenvironments is sampled within the same geographical area.

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Appendix

Taxonomic notes on the species studied.

Palaeospinaciformes

Synechodus levis (WOODWARD) (Fig. 3A): Although only a single incomplete tooth was collected during this study, several relatively large teeth of this species are present within museum collections. Described as *Hybodus levis*, examination of the type material has shown that the crown and root morphology is diagnostic of *Synechodus* and this species is therefore not a hybodont. Crown morphology may suggest close affinities with *S. pinnai* (DUFFIN 1987). *Synechodus* sp. (Fig. 4A-B): Teeth of this taxon differ somewhat from those of any species described from the Jurassic, and show a similar range of morphologies and crown ornament to *S. dubrisiensis* (MACKIE) from the Cretaceous. They may be separated from teeth of *S. dubrisiensis*, however, by the smaller number of lateral cusplets, greater degree of asymmetry of anterolateral teeth and more robust folds on the labial face of the root. Occasional specimens of larger, less ornamented teeth are tentatively assigned to large individuals of this species.

aff. *Welcommia* sp. (Fig. 3B-D): Superficially similar to '*Notidanus*' *serratus* (FRAAS), the detail of the single complete adult and several fragmentary juvenile teeth suggest an affinity with *W. terencei* DELSATE & GODEFROIT from which they can be separated by the presence of weak crown ornament. These Jurassic taxa differ from the Type material of *Welcommia* CAPPETTA in possessing well developed anterior cusps, and may require the establishment of a new genus. The inclusion of this taxon within the Palaeospinaciformes is tentative.

Hexanchiformes

? *Notidanoides* sp. (Fig. 4C): Although known from only a small number of fragmentary teeth, this taxon appears to compare well with other species of *Notidanoides* MAISEY. It is here considered that *Notidanoides* incorporates several species (WARD & THIES 1987) and should not be limited to the Type Specimen (as suggested in CAPPETTA 1990).

Heterodontiformes

Paracestracion sp. 1. (Fig. 4N-P): These small teeth differ from anterior teeth of *P. falcifer* (WAGNER) from the Late Jurassic in being more gracile and having greater numbers of well differentiated cusps. *P. sarstedtensis* (THIES) from the Early and Middle Jurassic differs in possessing longer cusps and a narrower crown. The differentiation of *Paracestracion* and *Heterodontus* by dental morphology has recently been described by UNDERWOOD (2002). No molariform lateral teeth were recorded, and it is possible that they were not present within this species. *Paracestracion* sp. 2. (Fig. 4Q): Very rare large and robust anterior teeth may be conspecific with teeth known from the British Callovian (MARTILL, 1991 pl. 38, figs. 1-2).

Heterodontus sp. (Fig. 4R-T): Anterior and anterolateral teeth have morphologies very similar to that of extant species of *Heterodontus*, distinguishing this species from *Paracestracion*. Anterior teeth are similar to those of the Late Jurassic *H. semirugosus* (PLIENINGER), but are considerably more gracile. Presumed lateral teeth are pectinate with a strongly concave labial edge, not closely resembling teeth of any other described heterodontid. No molariform lateral teeth were recorded, and it is possible that they were not present within this species.

Orectolobiformes

Orectolobid sp. 1. (Fig. 4G-I): Small teeth showing very strong heterodonty. High and asymmetrical anterior teeth resemble those extracted from skeletons of *Phorcynus catulina* THIOLLIERE, whereas more abundant lateral teeth are lower and more typical of *Hemiscyllium* SMITH. This taxon may require the establishment of a new genus. Orectolobid sp. 2. (Fig. 4J-L): These relatively robust teeth have an asymmetrical crown lacking well defined lateral cusplets and a concave labial face, and do not closely resemble any described orectolobid. This taxon may require the establishment of a new genus. Orectolobid sp. 3. (Fig. 4M): A single crown with weak ornamentation is unlike that of any described orectolobid genus.

Palaeobrachaelurus sp. (Fig. 4D): These teeth somewhat resemble those of *P. aperizostus* THIES 1983 from the Early Jurassic, but differ in the presence of a strongly convex labial protuberance.

aff. *Orectoloboides* sp. (Fig. 4E, F): Lateral teeth of this taxon strongly resemble teeth of *O. pattersoni* THIES differing in the possession of a weaker ornament and larger labial protuberance. Anterior teeth differ from those of any described species of *Orectoloboides* in having a crown overhanging the root, very well developed labial protuberance and labial ornament reduced to a single, or rarely multiple, longitudinal ridge. This taxon may be closely related to specimens recorded from the Toarcian and Aalenian by THIES (1989).

Carcharhiniformes

Palaeoscyllium sp. (Fig. 5A, B): Teeth differ from the Late Jurassic *P. formosum* WAGNER in having variably developed lateral cusplets and a finer ornament. Teeth with very low roots but very similar crown morphology appear to belong to this species and may indicate dignathic heterodonty.

'Scyliorhinid' sp. 1. (Fig. 5F, G): This taxon shows moderate heterodonty with the spaced ornament and incipient cusplets of juvenile and posterior teeth being absent in the majority of specimens. It is unclear whether a resemblance to teeth of some extant proscylliids implies a close relationship. 'Scyliorhinid' sp. 2. (Fig. 5C-E): More strongly heterodont than coeval 'scyliorhinids', this species has robust and weakly ornamented anterior teeth, with low and strongly ornamented posterior teeth. Lateral cusplets are absent from all teeth. It does not

closely resemble any described 'scyliorhinid' and may require the establishment of a new genus.

?*Palaeocarcharias* sp. (Fig. 4U): Two incomplete teeth are tentatively assigned to this genus, the affinities of which are uncertain.

Protospinaciformes

Protospinax sp. 1. (Fig. 5H-J): These teeth show considerable variation, with anterior teeth being larger and more cusped than other files. This taxon is known from the Callovian, anterior teeth from which have previously been described as *Protospinax ?muftius* by THIES, although the holotype appears to represent a separate orectolobid species. Lateral teeth have been figured as *P. annectans* WOODWARD by THIES (1983), but differ from the type material of *P. annectans* in the possession of a flat labial face, larger cusp and wider crown. *Protospinax* sp. 2. (Fig. 5K-M): Teeth are uniformly small with well-developed cusps in most files. The low root has a well developed nutritive groove in almost all specimens. This combination of features separate this species from any other member of the genus. *Protospinax* sp. 3. (Fig. 5N-P): This species may be recognised by possessing a narrow crown, high root and flattened, commonly 'V' shaped, basal face of the root. The poorly to moderately developed cusps invariably show extensive wear.

Rajiformes

Belemnobatis cf. *moorbergensis* (THIES). (Fig. 5Q, R): Some of the specimens recovered do not appear to differ from the type material, although show a greater degree of heterodonty, and generally possess wider labial protuberance. The nutritive groove is closed in most specimens. It is possible that more than one species is represented.

Spathobatis sp. (Fig. 5S, T): Larger than *B. cf. moorbergensis*, teeth of this taxon have a narrower crown, higher root and nutritive groove that may be either open or, especially in larger teeth, closed.

Rhinobatid sp. (Fig. 5U, V): These low teeth lack an occlusal crest and possess a conical cusp and small but clearly differentiated labial protuberance.

Figure Captions

Fig. 1.

Generalised Middle Bathonian palaeogeographic reconstruction of southern Britain showing main sample localities. Compiled from several sources and personal observation.

Fig. 2.

Distributions of Bathonian neoselachian taxa within different facies and their relative abundances.

Fig. 3.

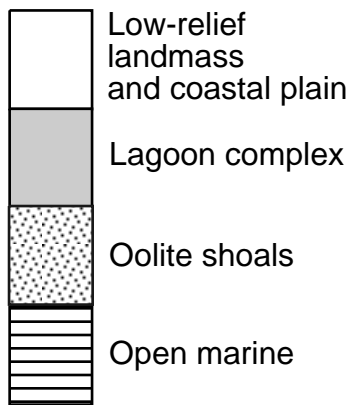
Larger Bathonian neoselachian teeth. Scale bar totals 6 mm. **A**, *Synechodus levis* (Woodward, 1889), labial view of incomplete tooth. **B-D**, aff. *Welcommia* sp., labial, basal and lingual views.

Fig. 4.

Bathonian neoselachian teeth. White scale bars for all species = 500 µm. **A**, *Synechodus* sp., labial view of posterolateral tooth. **B**, *Synechodus* sp., labial view of anterolateral tooth. **C**, ?*Notidanoides* sp., labial view of incomplete lateral tooth. **D**, *Palaeobrachaelurus* sp., labial view. **E**, aff. *Orectoloboides* sp., labial view of anterior tooth. **F**, aff. *Orectoloboides* sp., labial view of lateral tooth. **G**, *Orectolobid* sp. 1, labial view of anterior tooth. **H**, *Orectolobid* sp. 1, labial view of lateral tooth. **I**, *Orectolobid* sp. 1, labial view of anterolateral tooth. **J-K**, *Orectolobid* sp. 2, labial and lateral views of lateral tooth. **L**, *Orectolobid* sp. 2, labial view of anterior tooth. **M**, *Orectolobid* sp. 3, labial view. **N-O**, *Paracestracion* sp. 1, labial and lingual views of anterolateral tooth. **P**, *Paracestracion* sp. 1, labial view of posterolateral tooth. **Q**, *Paracestracion* sp. 2, labial view of anterior tooth. **R**, *Heterodontus* sp., lingual view of anterior tooth. **S**, *Heterodontus* sp., labial view of posterior tooth. **T**, *Heterodontus* sp., labial view of ?lateral tooth. **U**, ? *Palaeocarcharias* sp., labial view of abraded tooth.

Fig. 5.

Bathonian neoselachian teeth. White scale bars for all species = 500 µm. **A**, *Palaeoscyllium* sp., labial view of lateral tooth. **B**, *Palaeoscyllium* sp., labial view of anterior tooth. **C**, 'Scyliorhinid' sp. 2, labial view of anterior tooth. **D**, 'Scyliorhinid' sp. 2, labial view of posterior tooth. **E**, 'Scyliorhinid' sp. 2, labial view of lateral tooth. **F**, 'Scyliorhinid' sp. 1, labial view of anterior tooth. **G**, 'Scyliorhinid' sp. 1, labial view of lateral tooth. **H**, *Protospinax* sp. 1, labial view of anterior tooth. **I**, *Protospinax* sp. 1, lingual view of anterolateral tooth. **J**, *Protospinax* sp. 1, labial view of lateral tooth. **K-L**, *Protospinax* sp. 2, labial and lingual views of lateral tooth. **M**, *Protospinax* sp. 2, labial view of anterior tooth. **N-O**, *Protospinax* sp. 3, labial and lingual views of lateral tooth. **P**, *Protospinax* sp. 3, labial view of anterior tooth. **Q-R**, *Belemnobatis* cf. *moorbergensis* (THIES, 1983), occlusal and basal views of ?male lateral tooth. **S-T**, *Spathobatis* sp., occlusal and basal views of ?male tooth. **U-V**, Rhinobatid sp., occlusal and basal views.



Bathonian outcrop

